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Observations on Himalayan Tahr (Hemitragus jemlahicus)

BY

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(With two plates and a text-figure)

A small population of Himalayan tahr was observed on 20 days in eastern Nepal. Tahr used several vegetation types, ranging from broadleaved forest to alpine meadows between altitudes of 2500 and 4400 m, but their favoured habitat was grass-covered cliffs with patches of forest. Adult males outnumbered adult females by a ratio of 2:1; there were 56 young and 44 yearlings to 100 adult females. Tahr herds seemed to confine themselves to definite ranges. All members of herds were seldom together but congregated into unstable groups of varying sizes. Average group size was 6.5. Some adult males were with the females at the time of the study, some were solitary, and the rest were in small male groups. Tahr were most active before 0900 and after 1330 hours. Their principal food was grass, supplemented with browse. Courtship displays are described. Several indirect and direct forms of threat are used by tahr and these are described and quantified. Comparisons with Nilgiri tahr are drawn whenever possible. In their physical appearance, tahr represent a link between rupicaprids and the true goats of the genus Capra. This study shows that tahr also resemble both rupicaprids and true goats in their forms of aggression.

Himalayan tahr (Hemitragus jemlahicus H. Smith 1826) were successfully introduced into New Zealand in 1904. Anderson and Henderson (1961) published notes on the biology of these animals, and Caughley (1966, 1970, 1971) discussed their population dynamics in detail. Information on Himalayan tahr in their natural habitat consists only of general comments and hunting accounts (Burrard 1925; Stockley 1928), and even a description of the species' behavioural repertoire is unavailable

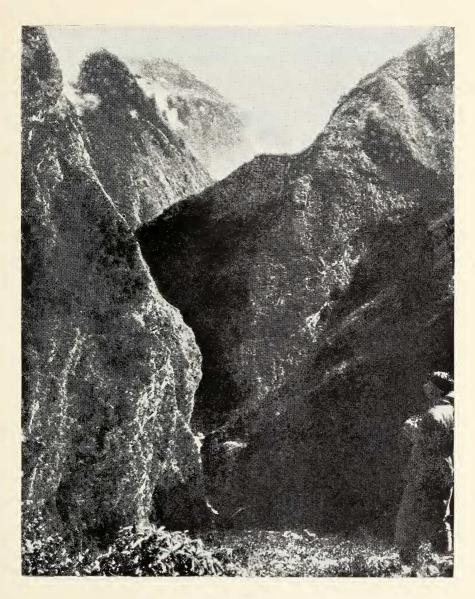
Between February 25 and April 5, 1972, I observed tahr on 20 days in and around the Kang Chu valley (also known as the Zom valley) of eastern Nepal. While my contact with the animals was limited to 80 hours of observation, the data contribute to the knowledge of the species and provide a basis for comparing the behaviour of Himalayan tahr with that of Nilgiri tahr (*Hemitragus hylocrius*).

The Kang Chu has its source in the Tibet province of China but soon crosses the border and flows southward through Nepalese territory for about 15 km before joining the Bhota Kosi river a stretch during which it descends from an altitude of 4000 m to 2500 m. A mountain range with peaks exceeding a height of 6000 m borders the valley on each side. At its confluence with the Kang Chu, the Bhota Kosi enters a canyon whose sheer cliffs rise 1000 m or more. After about 2 km the valley broadens, and soon after that, near the village of Lamobager, the river tumbles to lower altitudes. Tahr frequent most cliffs along the lower Kang Chu, the upper Bhota Kosi, and the adjoining Rongshar and Chyadu river valleys. I found tahr fairly abundant and observable only on the cliff that flanks the western bank of the Bhota Kosi between the mouths of the Kang Chu and Chyadu valleys (86° 14′ E., 27° 57′ N.). By climbing the cliff on the opposite side, I was able to observe tahr across the narrow canyon with a 20-power scope (Plate 1).

HABITAT

Himalayan tahr are found from the Jhelum river in the Pir Panjal Range of Kashmir eastward along the southern flanks of the Himalayas to about central Bhutan (Burrard 1925). Animals may occur from altitudes of as low as 1550 m in winter (Stockley 1928) to as high as 5300 m in summer (Caughley 1969). In the Kang Chu area, the species was observed between about 2500 and 4400 m, a range of altitudes which includes several vegetation types. The valleys and lower slopes up to an altitude of around 3000 m (the exact limit depending on degree of slope and exposure) are covered with a montane 'evergreen broadleaved forest' (Schweinfurth 1957). Although Quercus spp., Buxus wallichiana, and other trees may form almost monotypic stands, the forest usually consists of a variety of trees among which the genera Rhododendron, Magnolia, Acer, Alnus and Tsuga are prominent. Except for a few tall stands with a closed canopy beneath which there is little undergrowth, the trees are seldom more than 20 m high and the understory of saplings, shrubs, vines, and bamboo (Arundinaria) may be dense. Boulders often litter the floor and occasional cliffs break the continuity of the forest. Above the broadleaved forest is a belt of conifers and rhododendrons, with particularly fine stands growing on gradual terrain with a northern on north-eastern exposure. Fir (Abies) is the dominant

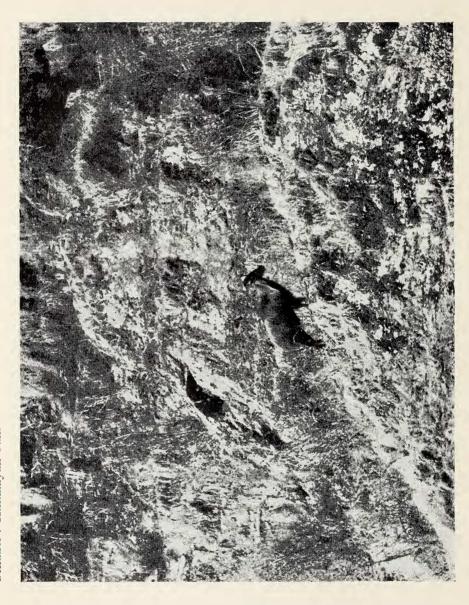
Schaller: Himalayan Tahr



The main tahr study area along the upper Bhota Kosi River, Nepal.

(Photo: George B. Schaller)

Schaller: Himalayan Tahr



A young adult male (class II) tahr on a typical ledge covered with grass and some shrubs. (Photo: George B. Schaller)

tree, and beneath it is a sparse understory of *Rhododendron* and *Betula*. At an altitude of about 3600 m the fir gives way to a stunted transitional zone of rhododendron, birch, willow and juniper, and it soon grades into the alpine vegetation of grasses, forbs, and mat-like shrubs. The line of permanent snow is at around 5600 m. Another habitat, one not recognized as distinct by Schweinfurth (1957), is found on cliffs, especially steep ones with a somewhat southern exposure. The faces of most cliffs are broken by many ledges and platforms which support much grass and occasional patches of shrub, bamboo, and broadleaved forest. With some cliffs rising for over 1000 m from the valley floor, this grassy habitat may grade into the alpine vegetation without an intervening forest belt.

The literature contains conflicting opinions about habitat preferences of tahr, although all authors agree that the animal 'revels in the steepest precipices' (Burrard 1925). Kinloch (1892). Burrard (1925) and others felt that tahr remain in forests and dense thickets, never ascending above timberline. Lydekker (1924), too, labeled them as 'essentially forest animals, 'but he noted that they may wander into the open. Prater (1965) held a similar view, and added that animals are never found outside thickets 'after the sun has well-risen.' In contrast, Caughley (1969), who observed tahr in central Nepal rather than in India as did the previous authors, stated that 'the habitat of this species is the subalpine zone between 3900 m and 5300 m.' I found tahr to be considerably more adaptable than these statements would indicate. Tahr frequented all habitats in my study area, although the conifer-rhododendron belt appeared to be used mainly in transit, perhaps because there was little food near ground level, especially in winter when snow was deep. The animals certainly were not adverse to open terrain. Old sign in the form of droppings and rest sites indicated that tahr spent much time above timberline during summer and autumn, and groups often remained on open cliffs throughout the day. In fact, tahr in New Zealand have adapted to tree-less terrain (Caughley 1970). The favoured habitat of tahr in the Kang Chu area, at least from February to April, was the grassy cliffs broken by small stands of forest and bamboo below an altitude of 3500 m. I suspect that the animals spent the winter there too, for the oaks and other evergreen trees provide forage as well as protection from bad weather. Furthermore, grass on cliffs is often accessible, the snow removed by wind and sun, while forests and alpine meadows remain deeply covered.

DESCRIPTION OF ANIMALS

Tahr differ from goats of the genus Capra in that both sexes lack a beard and have short, laterally compressed horns which curve sharply

backward. They resemble typical goats in their strong body odour and in the absence of pre-orbital, inguinal, and pedal glands on the fore-feet (Lydekker 1924). Male and female Himalayan tahr differ considerably in size and appearance, as do the sexes among most members of the tribe Caprini. I recognized several age and sex classes. The ages of subadults and of adult males were estimated on the basis of body size, pelage length, and other physical characteristics. It was sometimes possible to count growth rings on the horns of males. As Caughley (1965) has shown, one growth ring is laid down every winter of life after the first. The approximate ages are given as they were at the time of study.

Adult male (Class III), almost 5 or 6 years old and older. Males are handsome creatures with narrow, black faces and stocky bodies, the forequarters being particularly powerful. Their shoulder height ranges from 91 to 102 cm and their weight is around 90 kg (Lydekker 1924). Anderson and Henderson (1961) give similar figures for height of New Zealand tahr, but they estimate that some animals may weigh as much as 150 kg. The dark horns have a sharp keel in front. 'A well-developed set of bull tahr (sic) horns will measure 12-15 inches in length....and 8½-9 inches in circumference around the base' (Anderson and Henderson 1961). A male's most conspicuous feature is his ruff and mantle of flowing hair which drape from his neck, shoulders, and chest down to his knees and from his back and rump down to his flanks and thighs. The neck ruff is light brown in colour, as is the hair on each side of the dark mid-dorsal streak. There is also a light eyering and chin. The hair surrounding the anus is rusty in colour. The rest of the body is covered with a deep coppery brown to blackish pelage.

Young adult male (Class II), almost 4 years to perhaps 5 years old. Males of this age class resemble those in class III in size and in the presence of the shaggy ruff on neck and shoulders, but they are not as robust and the mantle of hair along the back is fairly short (Plate 2).

Subadult male (Class I), almost 3 years old. Class I males are only as large as or slightly larger than adult females. Their pelage is not as dark as that of adult males, and their horns are smooth and yellowish rather than corrugated and dark. Although a neck ruff is conspicuous, males of this class lack a mantle along the back.

Yearling male, almost 2 years old. Yearling males are smaller than adult females. In colour they resemble females, but they have a noticeable ruff.

Female, with a maximum weight of 36 kg (Anderson and Henderson 1961), adult females are considerably smaller than adult males. Their neck is yellowish brown in colour, except for a dark stripe along each side and along the mid-dorsal line. A light streak runs along each side of the back from the shoulders to the rump; the sides of the muzzle

also show a pale line. The abdomen is whitish. The rest of the pelage is dark brown. Some females have a small ruff but most have just a slight crest of hair on the back of the neck. The horns of females resemble those of subadult males in appearance, except that they are somewhat shorter and more slender. Yearling females are of the same size as yearling males, the most conspicuous difference between the two being that females lack a ruff.

Young, almost one year old. Young resemble yearlings, but they are considerably smaller, and, in the case of males, lack a ruff. Most young still followed and rested besides their mother even though they were weaned, judging by the fact that females discouraged occasional suckling attempts by stepping aside.

POPULATION DYNAMICS

Tahr were difficult to census because they were often out of sight in thickets. Although I often scanned the slopes of the Kang Chu Rongshar, and upper Bhota Kosi valleys, tahr were seldom seen, suggesting that they were scarce there. But there was one cliff along the Bhota Kosi, a huge pyramid-shaped one over 1 km long at the base and some 1000 m high, on whose face I readily found tahr. At least 45 tahr frequented this cliff, and, assuming a few were overlooked, the total was probably around 50.

TABLE 1
TAHR POPULATION STRUCTURE

	Structure ba number of di	A sed on known fferent tahr on y cliff	B Structure based on all animals tallied in study are		
	No.	%	No.	%	
Male III Male II Male I Yearl. male Adult female Yearl. female Young	2 3 4 4 18 4 10	4·4 6·7 8·9 8·9 40·0 8·9 22·2	14 14 17 28 93 18 62	5·7 5·7 6·9 11·4 37·8 7·3 25·2	
Total	45	100.0	246	100.0	

Table 1A shows the population structure of the 45 tahr on the study cliff. Since females limit themselves to distinct home ranges whereas adult males tend to wander widely (Caughley 1966), the percentages

are probably biased in favour of the former. Another way to analyze structure is to add up all tahr seen daily in the study area (Table 1B). This, however, skews data in favour of those animals which are met repeatedly. Nevertheless, the percentages derived by the two methods show close agreement. Adult females outnumbered classes I to III males by a ratio of about 2:1, in contrast to New Zealand tahr which seem to have a 1:1 ratio (Anderson and Henderson 1961). Fetuses examined by Caughley (1966) in New Zealand showed no disparate ratio. Male and female yearlings were represented equally in my study population. These facts suggest that males are perhaps not quite fully represented in the sample, solitary individuals being difficult to find, and that they may have a higher death rate than females, but I lack evidence on either point. Nilgiri tahr and Kashmir markhor (Capra falconeri cashmiriensis) also have a disparate sex ratio favouring females (Schaller 1970; Schaller and Mirza 1971).

Anderson and Henderson (1961) noted that some New Zealand tahr conceived as yearlings at the age of 18 months. The yearlings in my study population had slim abdomens, in contrast to the extended ones of adults, indicating that they were probably not pregnant. Himalayan tahr, in their natural habitat appear to have their first young at the age of 3 years. Males do not reach sexual maturtiy until at least 2 years of age, the testes of yearlings failing in most instances to increase in size and to produce sperm during the rut (Caughley 1971).

There was one pair of twins among 158 embryos examined by Caughley (1971) in New Zealand, and none in 66 examined by Rammell (1964). The 180 births in the New York Zoological Garden included one set of twins (Crandall 1964). Zuckerman (1953) reported on 115 births in the London Zoo and noted one pair of twins for every 12 births. Thus, single births seem to be the rule. Females in the Kang Chu had one voung at heel, except for one female which had two. Three young were with a female on several occasions, but these were temporary associations, the extra young joining other females later. Some 22% of the study population consisted of young, or 56 young to 100 adult females. Taking into account that several adult females had not yet had their first young and that an occasional female was perhaps barren, the figures suggest that around a third of the young had died between birth and the age of 8 to 9 months. Yearlings comprised 18% of the population, or 44 yearlings to 100 adult females, a good increment. With the tahr seemingly healthy and reproduction good, the population should be increasing unless an excessive number of adults die. I have no observations on causes of death. Some animals probably have accidents, and a few are no doubt killed by leopard (Panthera pardus), and, in the event that they straggle to the headwaters of the Kang Chu, by snow leopard (Panthera uncia). Meat hunters visit the area every summer,

according to the local Tibetans, and it is perhaps not coincidental that I found the densest tahr population on a cliff that is almost inaccessible to man.

HERD DYNAMICS

The tahr population on the study cliff was divided into two herds separated by a strip of forest, one using the northern portion, the other the southern. The females and young associated only with members of their respective herd, judging by the fact that several animals which I recognized individually were always on their usual part of the cliff, but some males may have wandered from one herd to the other. The northern herd contained at least 10 females and 5 young, the southern herd 12 females and 5 young. Several males of varying ages were with or near each herd. A third herd, seen only once on a slope opposite the study cliff, contained 9 individuals of which 3 were males. Members of a herd were seldom all together, being instead scattered in small groups which often joined and separated in various combinations in the course of a day. One dawn, for example, I spotted a group of 11 tahr, but by mid-morning it had split into groups of 4 and 7 which moved in opposite directions. A total of 36 groups (excluding groups composed solely of males) were classified during the study, a group being defined as two or more individuals separated by at least 200 m of terrain from others. Groups ranged in size from 2 to 23 with an average of 6.5, as compared with at least 22 members in each of the two study herds.

The basic social unit consisted of a female and her young. Such pairs roamed at times far from other herd members. Another common association included two or three females, a young or two, and often a yearling of either sex. Table 2 shows the composition of 3 large groups.

TABLE 2

THE COMPOSITION OF THE LARGEST GROUP IN EACH OF 3 HERDS SEEN DURING THE STUDY

Name of Herd	Male III	Male II	Male I	Yearl. Male	Adult Female	Yearl. Female	Young	Total
North	2 0 1	2	2	2	8	2	5	23
South		1	1	2	4	2	2	12
East		0	1	1	3	1	2	9

Nine out of 12 groups with 7 or more tahr contained at least one subadult or adult male. But, as is the case in many ungulate societies, contact between adult males and females outside the period of rut tends to be transitory. Males which were in a group in the morning had often left it by evening, going off singly and in twos or threes, perhaps to re-

join casually the following day. Even when such males were with a group, they often congregated at the periphery. For example, in the group of 23 (see Table 2), two class III males and one class II male fed and rested side by side near the others for several hours before leaving together. Eighteen per cent of the subadult and adult males I tallied were solitary or in twos. Stockley (1928) once observed a group of 6 male tahr and another time 24 of them together. Yearling males were usually with the females. However, on three occasions, a yearling was seen in the company of a subadult male far from any other group. Later in the season, contact between males and females may become even more tenuous. Caughley (1966), for instance, wrote that 'during the summer tahr range in three main kinds of groups: one consists of females, juveniles and kids, a second consists of young males and the third of mature males.' The males are said to join the females again in September prior to the rut (Burrard 1925).

The herd structure of Himalayan tahr resembled that of Nilgiri tahr (see Schaller 1970). In both species the herds tended to split into temporary groups and males had progressively less contact with the females after the rut. But there were two differences, at least in the populations I studied. The average group size of Himalayan tahr was 6.5 as compared to 23 in Nilgiri tahr. The latter species does most of its feeding on rolling grassland near cliffs. Such a habitat provides a concentrated and abundant food source, and this may well promote cohesiveness among herd members. In contrast, Himalayan tahr spend much of their time along narrow ledges where large groups would be at a disadvantage. Though average group size differs in the two species, average herd size possibly does not, but data on this point are lacking. Another difference between the species may be in the age at which males become solitary or join male herds. Some yearling Himalayan tahr, not quite 2 years old, had temporarily left the females, whereas Nilgiri tahr were not observed to join male herds until at least 3 years of age.

GENERAL BEHAVIOUR

Tahr spent most of the day feeding or resting, usually remaining several hours, or even a day or two, on a small section of the cliff. Only on a few occasions did a group move steadily for several hundred metres to another site. Sometimes animals travelled from a shady area until they reached one in the sun, and once they hurried away after boulders had crashed past them. At other times no reason for their movement was apparent. To obtain information about the activity pattern of tahr, I recorded the number of active animals every 5 minutes. The 6 points in each half-hour period were combined and expressed in per cent of animals active in the Figure which is based on 7146 activity observa-

tions between 0635 and 1730 hours. Tahr foraged and moved during all daylight hours, but there were peaks of activity before 0900 and after

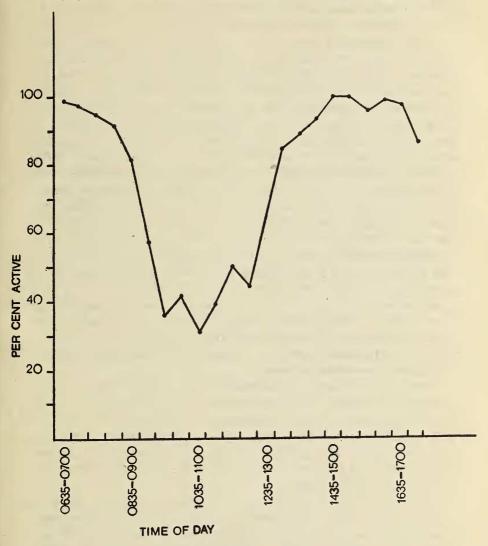


FIGURE. Per cent of tahr active at various times of day, 0635 to 1730 hours.

1330 hours. Although tahr were, in general, least active from midmorning to early afternoon, the same groups sometimes varied considerably in their foraging pattern from day to day, often without obvious cause. Weather, however, may affect activity. On several occasions a group rested while the sky was clear, then began to forage as soon as it became cloudy. Groups seldom reclined for more than an hour or two without at least one member feeding, and, in large groups, there was usually some activity from dawn to dusk.

Tahr had a limited selection of food plants available at the end of the winter. Oak leaves were eaten whenever a group was in a forest patch. To reach low-hanging leaves, an animal may rear up on its hindlegs and bend and hold down a branch with one or both forelegs while browsing rapidly. Once a subadult male leaped 2 m into the fork of a tree, behaviour common in foraging Kashmir markhor but not tahr. Bamboo was also an important food, but the abundant leaves of rhododendron were seldom sampled. The tahr's principal food was dry grass. In late February animals spent hours foraging on Danthonia schneideri, Cymbopogon thwaitesii, Arundinella nepalensis, and other species. After obtaining a mouthful in one or more bites, an animal characteristically raised its head and chewed. I recorded the type of vegetation selected by two male tahr on two days in February. Of 155 mouthfuls, 75% consisted of grass, mainly wads of dead leaves and stems bitten off at the base, 7% of twigs and leaves from several shrubs and saplings, 6% of bamboo, 4% of dry forbs, and the rest of unidentified material which was at time obtained by first pawing the ground. By early March, green grass shoots became conspicuous, and tahr nibbled these. Yet dead grass continued to be eaten, even late in March when much green forage was available. Newly sprouted leaves of Polygonum molle, Leucoceptrum canum and other forbs and shrubs were at that time also a part of the diet. One tahr ate the blossoms of Daphne gracilis, and several others appeared to lick crustose lichens off rocks.

From mid-February to mid-March, when average daily minimum temperatures hovered around the freezing point, tahr tended to forage in the forest during the early morning hours. Not until sun reached the cliff, usually around 0830, did they venture into the open. But during the second half of March, when the average minimum temperature was 6°C, tahr were out at dawn, and, in fact, they may not have retreated into the forest at all during the night.

To reach the scattered patches of vegetation, tahr have to be good climbers, and, indeed, they traverse ledges and rock faces with an adeptness that can have few equals among ungulates. Their hooves are well designed for gripping rocks. 'The hoof pads are very soft, slightly convex posteriorly and surrounded by a hard horny rim which must serve a similar purpose to that of nails around the outside edge of mountaineers boots' (Anderson and Henderson 1961). Further traction is provided by the large dew claws. Tahr readily balance along ledges only a few centimetres wide and may leap with precision onto a small grass tussock growing on a sheer cliff 2 m below them. When confronted by a smooth, sloping rock face, an animal may rock back and forth and suddenly propel itself upward with a series of leaps, using the callus on each

knee rather than the hooves to grip the rock fleetingly. The tahr's breast is calloused too according to Blanford (1888-91). Callus-like areas are also present on the hocks and these are used to supplement the hooves as brakes when an animal slides in a squatting position down a steep incline.

During rest periods, tahr reclined on exposed ledges, on rocky spurs, in thickets, almost any place which offered some level terrain; animals also retreated beneath rock overhangs when such were available. On warm days, when shade temperatures reached 15 to 20°C, some tahr rested beneath trees yet others remained in the sun. Windy places were not avoided, and a male often rested on a promontory with his mane whipping in the breeze. 'It is common for a group of tahr to have one or two sentinels posted,' according to Anderson and Henderson (1961), but I saw no evidence of this. Tahr were never seen to paw the ground before lying down, behaviour which is, for example, conspicuous in markhor (Schaller and Mirza 1971). Animals either reclined with all legs tucked beneath the body or with one or both forelegs stretched forward. Cud-chewing was intermittent. Two subadult males were timed as they chewed a total of 25 boli. The average number of chews per bolus was 78 (65-87), and the time required to chew each bolus was 49 (40-65) seconds.

TABLE 3

AGE AND SEX OF TAHR INVOLVED IN LICKING INTERACTIONS

			Anin	nal being l	icked		
Animal licking		M	lale		Fen	nale	Young
	III	II	I	Yearl.	Adult	Yearl.	
Male III Male II Male I Yearl. male Adult female Yearl. female Young	1		3 1	11	1 11 7 3 8	3	12

Tahr sometimes interrupted their rest or search for forage to groom themselves, licking their pelage and scratching it with hindleg or horntip. Social grooming, with one tahr licking the head and neck of another, was observed on 61 occasions. An interaction may be cursory, limited to a few licks, but it may also last for as long as 10 minutes. Licking was often reciprocal, with, for instance, a female first licking her young and then being groomed in return. On a number of occasions an animal

invited licking by holding its head close to the muzzle of another. As Table 3 shows, most licking involved either two females or a female and a young; subadult and adult males seldom licked each other. Most interactions between adult females and yearling males, as recorded in Table 3, took place between the same pair of animals. Social grooming was a conspicuous activity among Himalayan tahr but not Nilgiri tahr, a difference for which I have no explanation.

REPRODUCTIVE BEHAVIOUR

The duration of the tahr's rut in the Himalayas is unknown, but since the gestation period is $6\frac{1}{2}$ months (Caughley 1971), and young are born either in May and June (Stockley 1928; Prater 1965) or June and July (Blanford 1888-91; Lydekker 1924), most mating must take place between mid-October and mid-January. The age difference between some young in my study population was at least two months, and, in New Zealand, Caughley (1971) noted that births were spread over a period of almost three months. I saw a few instances of courtship behaviour and one copulation long after the termination of the main rut, and my notes are summarized here.

Males showed several behaviour patterns only in response to the presence of females:

Lip-curl: On 5 occasions a male either sniffed the anal area of a female or the spot where she had recently rested and then lifted his muzzle high with the upper lip curled. Yearling, class I, and class II males behaved in this fashion.

Low-stretch: A male may approach a female with his neck lowered and almost parallel to the ground and with his muzzle directed ahead or slightly raised. Males typically come up behind females in this way and sniff their anal area. This display, which is common to many ungulates, has in tahr become further elaborated. By raising the muzzle until it points almost straight up and retracting the neck, the shoulders of the male are transformed into a hump. Instead of remaining behind the female, the male now faces her rigidly, a position which exposes the front of the neck ruff to best advantage. His tail may be raised vertically and his teeth bared. Standing there, he may lift his muzzle higher and higher until it reaches above the level of his hump. This posture resembles the head-up display, with head raised and neck erect, of some ungulates (Walter 1961; Geist 1971).

Twist: While approaching a female in the low-stretch, a male may twist his head so that his horns point away from her. This gesture was seen twice,

Tooth-baring: As he faces a female in the low-stretch, a male sometimes retracts his lips to expose his incisor teeth and gums whose whitish colour contrasts markedly with the black lips and nose. It is possible that this gesture is an exaggerated form of lip-curling. If so, its function has been extended from one mainly designed to test the estrous state of the female by olfactory means to one of display value.

Head-shake: A male may interrupt the low-stretch in front of a female and jerk his head down, as if nodding vigorously, all the while shaking it rapidly from side to side. Then he resumes his former posture, often to shake again a few minutes later. One male displayed behind a female in this fashion.

Tongue-flick: As a male shakes his head, the tongue usually flicks rapidly in and out of his mouth. This gesture may also be displayed when a male follows an estrous female and when he faces her in a low-stretch.

Kick: During the head-shake, a male sometimes lifted a foreleg some 15 cm off the ground and kicked it limply and slightly bent at the carpal joint. Such kicks did not touch the female.

Males possibly add further emphasis to their displays by vocalizing, as noted in several goat species by Walther (1961), but I was too far away to hear sounds.

To place the display patterns into their natural context, the only lengthy courtship I witnessed is here described in a condensed form. The same animals were presumably involved, but I am not certain of this.

March 24. A group of 16 tahr is scattered over a cliff. At 1050 hours, a class II male approaches a female and gives the low-stretch in front of her. He stands with muzzle raised and head turned to one side for 5 minutes before he shifts his gaze to face her directly. She has her neck lowered and muzzle pointed downward. Soon he assumes a similar posture. (Both the averted glance and lowered head seem to be gestures of submission, showing lack of aggressive intent). After a few minutes the female suddenly jabs him lightly in the neck, but he merely lowers his head still more. Both stand motionless. When the male raises his head, she jabs him again, and he promptly assumes his former position. One hour after meeting the female, the male gives an intense low-stretch, muzzle straining skyward, then turns aside, licks himself, and ambles off. A class III male has been lying in full view 30 m away. He now displays the low-stretch to the female, grazes by her side a few minutes, then drifts off too.

March 25. At 0815, a female is attended by a class III male and two class II males, all somewhat separated from the main group. When a class II male approaches the female, the class III male by her side ad-

vances toward him in a hunch display (see below). The smaller male turns aside, joins the other class II male, and both rest at least 10 m from the courting pair. The class III male assumes the low-stretch, but the female ignores it and he reclines. At 0910 hours the approach of a class II male brings him to his feet, and a hunch display causes the interloper to veer off. Once again he faces the female in a low-stretch. For 15 minutes they stand, he with muzzle raised, she with head averted. After that both feed and rest. At 1105 hours, the female approaches the male who lifts his muzzle so high that the underside of his jaw faces her. licks herself, advances, licks again. Whenever she moves, he adjusts his position so that his muzzle points at her. Suddenly he steps behind her, his shoulder by her rump. He gives a low-stretch coupled with a twist, then shakes his head and kicks. Twice more he shakes and kicks before moving around to face the motionless female. There he alternately low-stretches with teeth bared and shakes a total of 9 times. Occasionally he nudges the female with his nose as if to get her attention, for when she looks at him he intensifies his low-stretch. The female begins to feed at 1200 hours. Slowly the male steps behind her and rears on his hindlegs, mounting her. He thrusts 10 times, barely leaning against her, without eliciting a response. The two then feed and rest near each other without further courting for several hours.

March 26. I spot the tahr at 0800 hours. A class II male is giving the low-stretch with teeth bared to a female. Above the pair on a ledge is a yearling male and a young. The yearling butts the young so hard that it falls 2 m and collides with the courting male. Although he is nearly knocked off his feet, he calmly resumes his displaying. He alternately low-stretches and shakes, also giving occasional kicks and flicks of the tongue. Once he and the female touch horns. Between 0800 and 0835 hours he has 74 bouts of head-shaking. The female just stands, her head turned aside, but twice she jerks her horns at him aggressively and once butts his shoulder. At 0835 hours she walks off out of sight, followed at a distance by the male.

Of particular note is the gentleness with which courtship was conducted. The males did not press their attention on the female, but limited themselves to displaying and lingering nearby. Although I saw only one prolonged courtship, other observations suggest that it was a representative one. A class I male once followed a female closely for two hours, obviously interested in her yet never approaching closer than 1.5 m. Low-stretch displays, sometimes accompanied by tongue-flicking, teethbaring, and, on one occasion, by kicking, were observed a total of 17 times on 10 different occasions, in addition to the instances related above. Fourteen of these displays were given by yearling males and the rest by subadult and adult ones. Females usually ignored such displays, but on two occasions, when importuned by a yearling, they rebuffed

them. Once, when a yearling gave a low-stretch to a female, she jabbed him in the neck. He persisted and was rewarded with a poke in the rump. He in turn pressed his forehead against the base of her neck, a position which prevented her from horning him effectively. After a few futile jabs, she stepped aside and hooked his neck, and, as he turned to leave, his side too. Undaunted, the male displayed again, only to be butted in the shoulder. But all such attacks lacked vigour, they were limited to fairly gentle jabs. The males in turn did not retaliate, except twice to butt a female. On 9 occasions a pair also locked horns and tussled briefly and lightly. Alpine ibex (Capra ibex) and mountain sheep (Ovis canadensis) also court cautiously (see Geist 1971). Aside from other considerations, there would seem to be selective advantage in courting with restraint on cliffs.

Anderson and Henderson (1961) wrote that in New Zealand tahr 'the typical family group consists of a bull, a nanny, its kid, and either the offspring of the previous year or a 2-year-old, and together they move to a well-chosen piece of territory to remain for some 6 to 8 weeks.' Such 'monogamous grouping,' as these authors call it, was not evident in the one courtship I witnessed. Rather the largest male in the group claimed the estrous female, a pattern similar to that observed in markhor (Schaller and Mirza 1971) and ibex (Nievergelt 1967).

AGGRESSIVE BEHAVIOUR

Anderson and Henderson (1961) were impressed with the placid nature of tahr, noting that 'a more docile assembly would be hard to visualize.' While it is true that fighting is relatively uncommon, at least outside the rutting period, tahr do interact aggressively in a number of ways, using both direct and indirect forms of threat. Among the overt types were the following:

Jerk: A tahr may jerk down its head and point its horns at an opponent. The gesture signifies an intent to butt, and the threatened animal usually retreats a little. It was seen 15 times, directed mainly by females at courting males (6 times) and at young (4 times).

Lunge: On 3 occasions a female jerked down her head and at the same time lunged a metre or two at another animal, twice at a female, and once at a yearling male.

Jump: A young reared up on its hindlegs in front of another young on two occasions. A jump probably represents an intention movement to clash with a downward thrust of the horns.

Butt: Butting was the most common form of aggression in tahr. It consisted either of a push with the blunt edges of the horns or of a jab

with the tips. The attack was directed at the neck of the opponent 8 times, the shoulders and sides 8 times, the thighs 3 times, and rump 5 times. Females delivered most butts, usually to courting males; and young butted each other several times seemingly in play. However, butting also occurs in serious fights as described by Roberts (1971):

'While observing the movements of a group composed of a mature bull, ten females and young, my attention was drawn to a large, lone bull about 500 feet above this herd when he started to smash into the turpentine scrub with hooves and horns and moved downhill towards the bull with the females....The two bulls confronted each other, whistled sharply, and began to wrestle like domestic cattle. The tactics appeared to be to try to put the opponent off balance, for after a period of pushing, twisting, and sliding downhill one bull was heaved off balance and the victor immediately shot his horns under him and ripped him in the belly. This upset him, and he tumbled down into the steep gully.'

Clash: On 18 occasions two tahr clashed horns, or, in the case of young, primarily foreheads. Sometimes one animal took the initiative, the opponent merely catching the blow with the horns, but at other times both jerked down their heads in unison. With locked horns they then twisted their heads and pushed each other back and forth. Two to four clashes sometimes followed in quick succession. None were violent and all were brief. Yearling males and females clashed most often, usually after the former had displayed the low-stretch. Once a young approached a yearling male playfully with its head low and waving from side to side until their horns met. A yearling male and a yearling female sparred gently 3 times, and two young clashed twice. Probably Himalayan tahr also rear up on their hindlegs in unison and lunge downward to clash their horns forcefully in the manner of Nilgiri tahr, ibex, markhor and other goats, but I did not see such behaviour.

Head-to-tail: Two young once stood parallel and head-to-tail as they hooked at each other's sides. On two other occasions a female and yearling male assumed similar positions, but circled rapidly with their heads cocked as if to jab. This method of fighting is similar to the one I termed shoulder-push in Nilgiri tahr except that the animals did not shove with their bodies.

As Table 4 shows, the various age classes differed in the amount of overt aggression. In 106 animal-hours¹ of observation, class I, II and III males asserted themselves only 5 times. Females were also unaggressive except when being courted. Young had a fairly high aggressive

¹ One animal observed for one hour equals one animal-hour.

TABLE 4

TYPE AND FREQUENCY OF OVERT AGGRESSION USED BY VARIOUS AGE AND SEX CLASSES OF TAHR

Age and sex class	Jerk	Lunge	Jump	Butt	Clash ¹	Head-to-tail Total no. Aggressions	Total no. Aggressions	No. aggressions per animal-hour of observation
Male III Male II Male I Yearl. male Adult female Yearl. female	2 1 1 4 (6)	m	7	1 (2) 2 (12), 1 5	(1) 6 (9) 1 (10) 3	(3) (3)	0 22 41 4 16	0 06 (03) 05 11 (19) 04 (14)

¹ In the clash and head-to-tail interactions both participants are included in the tabulation because both behaved aggressively. Interactions during courtship are tabulated separately in parentheses. The data are based on 603 animal-hours of observation of tahr in groups.

rating, though some of their behaviour was playful, and yearling males had the highest. The goat-like blue sheep (*Pseudois nayaur*), which I observed during the same period as the tahr, showed a similar pattern of aggressive frequencies, except that young rated low (Schaller, in press). With respect to Nilgiri tahr, Schaller (1970) noted: 'A ranking of the classes based on relative frequency of fighting would place light brown males [classI] at the top, followed in decreasing order by yearlings, females, dark brown males and saddlebacks [classes II and III] and young.' The phase of a species' reproductive cycle has, of course, a considerable influence on aggressive frequencies. Schaller and Mirza (1971), for example, found that rutting adult male markhor were more aggressive than any other age and sex class.

Direct threats were mainly used by females toward individuals smaller than themselves, by one young toward another, and by courting pairs. Males, on the other hand, tended to employ various indirect forms of threat to intimidate each other as this example illustrates: After approaching to within 25 m, a subadult and yearling male halted and horned vegetation with vigorous sweeps of their heads, one using a grass tuft, the other bamboo. The subadult male then slowly came closer, once stopping to lick himself. Meanwhile the yearling grazed intensively. When the subadult had approached him to within 1.5 m, he licked and scratched himself, fed again, and groomed once more, a changing pattern he repeated 4 times. The subadult also groomed himself. But suddenly he hunched his back and stalked stiffly past the yearling. After that both foraged, drawing slowly parallel. They halted broadside to each other, standing motionless for 15 seconds with heads slightly lowered and averted before parting.

Horning vegetation: Nine instances of horning were observed, 5 of them by yearling males and the rest by subadult and adult ones. Some males horned during aggressive encounters, as the above example shows, but others thrashed vegetation in no particular context.

Hunch: On 5 occasions a subadult or adult male hunched his back, bunched his legs stiffly beneath him, lowered his neck either in an extended or retracted position, and pointed his muzzle obliquely downward. His tail was raised vertically, as in some low-stretch displays, exposing the small rump patch. The anus appeared puckered outward. With the hair on his nape and shoulders more erect than usual, he may walk or trot at another male in this posture, resembling a huge shaggy grass tussock with a black face peering from it. The threatened animal promptly avoided this apparition. At other times, the displaying animal walked broadside to his opponent, a position which did not cause immediate retreat.

Broadside: One tahr may stand close to another with its neck stretched somewhat forward, and with its muzzle held horizontally or tipped slightly up or down. Geist (1971) illustrates this posture in his book. The displaying animal either stands parallel to the other and facing in the same direction, a position which shows off the size of the ruff, or it halts in front or behind the other. A conspicuous feature of the display is that the muzzle is seldom pointed directly at the opponent but is averted to show a partial to complete profile. The threatened individual often responds by assuming the same posture with the result that the two display side by side or face to face, a metre or two apart, each with its muzzle turned away. I observed this display 7 times, once between 2 yearling males, 4 times between a subadult and a yearling male, once between an adult male and a yearling male, and once between an adult and yearling female. Most contacts were brief, lasting less than a minute, but on one occasion a subadult and a yearling male displayed to each other 3 times within a period of 50 minutes, each interaction lasting some 5 to 10 minutes. An animal sometimes terminated such an interaction by licking or scratching itself before turning away.

Tahr often groom themselves in conflict situations such as during courtship, when one male meets another, and when displaying broadside. For instance, during the brief meeting between the two males described earlier in this section, the subadult male groomed himself 7 times, but he did not lick or scratch during the 30 minutes preceding the interaction and only once in the hour succeeding it. A courting female groomed herself 19 times in 6 hours, usually when the male displayed to her. By indulging in an innocuous activity such as licking, tahr seemed to find relief from a tense situation or were able to terminate a confrontation without having to retreat abruptly.

DISCUSSION

In their physical characters, tahr appear to be evolutionary links between the rupicaprids or goat-antelopes, of which American mountain goat (*Oreamnos americanus*) and chamois (*Rupicapra rupicapra*) are well-studied representatives, and the true goats of the genus *Capra*. It would be of interest to find out if tahr are behavioural as well as morphological links, and this can best be done by comparing the courtship and aggressive displays of *Hemitragus* with those of various goats and rupicaprids. Schaller (1970) made a few such comparisons, and this account provides further information.

Treating first courtship among rupicaprids, Geist (1965) found that male mountain goats approach females from behind in a low-stretch, sometimes with tongue flicking. This may be followed by a vigorous kick that propels the female forward. 'If the female turns in horn-

threat on him, the male turns his head away from her, and thereby shows the broadside of his face and beard' (Geist 1965). The low-stretch of mountain goats is less elaborate than that of tahr, but with the kick the reverse is true. Male mountain goats may sit on their haunches and paw 'rutting pits', as Geist (1965) called them, behaviour not seen in tahr. Among chamois, the male approaches a female in a low-stretch, and then 'the courting billy stands behind the nanny with his head erected, thereby displaying his white throat' (Krämer 1969). Lip-curling is common among chamois, but kicking, twisting and other patterns found in tahr are not mentioned in Krāmer's detailed account. Rutting male chamois may shake their body vigorously and at the same time urinate with the result that fluid is sprayed over their pelage. The courtship displays of ibex, tur (Capra caucasica) and markhor are similar to those of Himalayan tahr in many respects (Table 5). However, some variations exist even in those displays which are found in all these species. When kicking, for example, Kashmir markhor tend to raise the leg fairly stiffly for a few centimetres, Alpine ibex may make pawing movements with their flexed foreleg (Walther 1961), and Himalayan tahr merely raise a leg limply, bent at the carpal joint. Head-shaking, so typical of courting Himalayan tahr, has not been reported in Capra, but ibex shake their head in a somewhat different manner as a form of threat (Walther 1961). A rutting Capra male typically urinates on his forelegs and face, and he may insert his penis into his mouth. Although tahr were not seen to do this, it is possible that such behaviour occurs during the rut. As Table 5 shows, some displays, such as the low-stretch, are found in all species listed, and, in fact, tend to be widespread among ungulates, whereas others are unique to one species. In general, the two rupicaprids appear to have fewer courtship patterns than members of the genus Capra, and Himalayan tahr share more displays with the latter than with the former. Nothing is known about courtship in other species

It is necessary to note similarities and differences in the aggressive behaviour of Himalayan and Nilgiri tahr before fruitful comparisons with other genera can be made. Jerking, lunging, jumping, butting, frontal clashing, and horning are similar in the two species, but several differences also exist. At times two Nilgiri tahr 'stood parallel and facing the same direction and in unison jerked their head sideways rapidly once or twice thereby clashing their horn against one of the opponent's' (Schaller 1970). Such behaviour was not observed in Himalayan tahr. Both species horn while standing head-to-tail, but, in addition, Nilgiri tahr push with their shoulders and may kneel while fighting. The hunch differs somewhat in the two tahr: in the Nilgiri species the neck and head may be arched so far down that the muzzle points back between the legs, whereas in the Himalayan species the neck and head are merely stretched

TABLE 5

inae	Tur (Steinhauf 1958)	++ ~ ++ ++ +
SUBFAMILY Capr	Alpine ibex (Walther 1951)	++ + ++~++ +
SEVERAL SPECIES OF THE	Mountain goat Chamois Markhor Alpine ibex Tur (Geist 1965) (Krämer 1969) (Schaller & Mirza 1971) (Walther 1961) (Steinhauf 1958)	++ + ++++ +
IIP PATTERNS IN	Chamois (Krämer 1969)	++ ++ +
E MALE COURTSE	Mountain goat (Geist 1965)	++ ++ +
THE OCCURRENCE OF SOME MALE COURTSHIP PATTERNS IN SEVERAL SPECIES OF THE SUBFAMILY Capringe	Himalayan tahr Mountain goat Chamois (this study) (Geist 1965) (Krämer 196	++++++ ~~~
	Pattern	Lip-curl Low-stretch Tooth-baring Twist Head-shake Tongue-flick Kick Head-up Urinating on body Unserting penis in mouth Digging rutting pit Body-shake Tail folded over rump

obliquely downward. Possibly the accentuated body posture of Nilgiri tahr is an evolutionary alternative to having a prominent display structure, such as the ruff of Himalayan tahr. I saw no display resembling the broadside of Himalayan tahr in Nilgiri tahr, but more work will no doubt clarify whether differences between the two species are qualitative or merely quantitative.

Mountain goats and chamois both jerk, lunge, jump, and butt. The former do not clash (Geist 1965) and the latter clash seldom (Krämer 1969), probably because their thin, pointed horns are unsuited to such activity. Animals with massive horns commonly clash, a fact true also for takin (Budorcas taxicolor), which usually are considered to be rupicaprids. All Capra, as well as blue sheep (Pseudois) and tahr clash not only by facing an opponent on all fours and bashing horns, but also by rearing upright in unison and with a downward lunge crashing horns together. Interestingly, Krämer (1969) reported this type of combat in chamois, indicating that such behaviour is not confined to the tribe Caprini as was previously assumed. The head-to-tail method of fighting was observed in young chamois by Krämer (1960). And Geist (1965) noted an analogous pattern in mountain goats: 'They fight keeping side by side while moving about one another. Goats strike up and sideways with their head, driving the horns into the opponent's ventral body region.' This display, common to both tahr species, has not been described for Capra, although domestic goats may stand side by side and push each other with the shoulders (Geist, pers. comm.). Neckpushing, a form of combat in which one animal places its neck over the neck or shoulders of another and pushes downward, has been observed in young chamois (Krämer 1969) and in adult Ammotragus lervia (Haas 1959), a species intermediate between sheep and goats. Such behaviour has not been reported for Hemitragus and Capra.

Turning to indirect forms of threat, the mountain goat has a hunch posture which resembles the one described earlier for Nilgiri tahr. The hunch of the chamois is similar to that of the Himalayan tahr. Chamois present their broadside with humped back and either lowered or raised head, showing off their dorsal ridge of hair. Males may lip-curl in this posture, having apparently incorporated a sexual pattern into a threat one (Krämer 1969). The takin also exhibits the hunch display. The three Burmese animals in the Bronx zoo commonly arch their neck far down with chin tucked in and ears retracted, and moving stiffly, present their broadside. The head is often slightly averted and snorts may be given. The hunch in all these species is a broadside display, serving to intimidate an opponent by presenting a conspicuous profile. However, Himalayan tahr have an additional broadside display distinct from the hunch. It was my impression that this tahr sometimes used the hunch as a direct threat, rather than only as an indirect one as is the case in